A CONTROL MODEL OF THE VESTIBULAR SYSTEM

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ABSTRACT

The human vestibular system for dynamic space orientation is described mathematically, using the identification methods of control theory. A biocybernetic model is useful in predicting man's perceived orientation in space, postural reactions, nystagmus eye movements, and piloting actions based on motion cues. The semicircular canals, which act as angular velocity sensors, have been subjected to a fluid dynamics analysis. The limitations of the torsion pendulum model are examined, and a quantitative description of adaptation is proposed. An otolith model, responding to linear acceleration forces, is presented and shown to agree with perception of tilt and translation, eye counterrolling, and electrophysiological data. Cross-coupling effects are discussed, including the influence of linear acceleration on the semicircular canals.

INTRODUCTION

The control systems engineer views the vestibular apparatus both as a potential problem and as a challenge.[1,2,3] The problem stems from the use of vehicles to expose men to other than the normal environment for which the vestibular system was designed, resulting in such man-machine interface difficulties as vertigo, disorientation, and motion sickness. The challenge comes in attempting to recreate mechanically the elements

of an attitude control system or short term inertial guidance system of the size of the nonauditory labyrinth.

This paper presents our attempts to develop mathematical models for the functioning of the vestibular system, much in the manner of a control engineer examining the dynamic characteristics of the sensors of a feedback system. Such models, of course, indicate only average responses and are a guide to interpreting experiments. The overall framework for our investigation is shown in Fig. 1, in which the vestibular responses form parts of the postural feedback loops, the vehicle orientation feedback loop for the pilot situation, and the visual feedback loop via the mechanism of vestibular nystagmus. The emphasis of this paper is two-fold. Primarily it exposes the analysis and experiments which have been applied in the course of developing mathematical models of the semicircular canals and otoliths. These methods are typical of the techniques being used throughout the field of biological control systems. Secondly, the paper points out those special areas where the control systems analysis has raised important questions directed to the physiologist. In the constant attempt to develop a model which explains behavioral "input-output" data and is consistent with the known physiological structure, the model serves its purpose in pointing out the new areas for investigation, posing testable hypotheses.

SEMICIRCULAR CANALS

Current theories for the operation of the semicircular canals stem from the classic work of Steinhausen in 1931 based in part on his direct observations of the deflection of the cupula in the pike when it was undergoing angular accelerations.[4] As seen in Fig. 2, each canal originates from a common sac, the utricle, forms a rough semicircle, and then returns to the other end of the utricle.[5] The operation of each semicircular canal may be viewed as the mechanical action of a torsion pendulum. The moment of inertia of such a pendulum corresponds to the moment of inertia of the fluid ring in the canal. The damping term results from the viscous forces related to endolymph flowing through the canal, and the elastic restraining force is attributed to the springiness of the

Superior numbers refer to similarly-numbered references at the end of this paper.

cupula which is displaced from its neutral position by any movement of the endolymph. Early attempts to ascertain the parameters of the second order equation describing the torsion pendulum were carried out extensively at Utrecht and summarized by Van Egmond, Groen, and Jongkees in 1949.[6] Using their original notation, we find that the differential equation for angular deviation of the endolymph in relation to the skull, and therefore angular deviation of the cupula, is given by

$$\theta \ddot{\xi} + \pi \dot{\xi} + \Delta \xi = \alpha \theta$$

where

θ = moment of inertia of the endolymph

π = moment of friction at unit angular velocity of the endolymph with respect to the skull

Δ = stiffness, or torque moment per unit angular deflection of the cupula

ξ = angular deviation of the endolymph with respect to the skull

α = component of angular acceleration of the skull, with respect to inertial space, normal to the plane of the semicircular canal

Using this model with appropriate values of the parameters π/θ and Δ/θ, the cupula position can be predicted for a variety of forcing functions of angular position applied to the head: for example, constant acceleration, sinusoidal oscillation, and an impulse of acceleration resulting in a step change in angular velocity.

Steer recently completed a detailed fluid dynamic analysis of the motion of endolymph in a rigid torus of the dimensions of the semicircular canal, assuming no flow at the surface of the canal and initially no cupula present (see Fig. 3).[2] Solution of the Navier-Stokes equations for fluid flow following a sudden angular acceleration results in the expression

$$v^2(r, z, t) = \sum_{i=1}^{\infty} [C_i \ Z_i(A_i r)\cos B_i z \ e^{(\lambda_i)^2 \frac{\mu}{\rho}t}]$$

where

$Z(A_i r)$ represents first order Bessel functions and

$$(\lambda_i)^2 = A_i^2 + B_i^2$$

The coefficients C_i and λ_i may be arrived at by considering the boundary conditions and the equation expressed as a transfer function in Laplace notation:

$$\frac{\overline{v}(s)}{\alpha(s)} = D \sum_{i=1}^{\infty} [\frac{D_i}{\tau_i s + 1}]$$

where

$$\tau_i = \frac{(\lambda_i)^2 \mu}{\rho}$$

$\overline{v}(s)$ = mean fluid velocity

$\alpha(s)$ = angular acceleration

The detailed analysis then reveals that the effects of viscous drag and moment of inertia in the semicircular canals can be represented by the parallel actions of a sum of first order lag networks. 96% of the effect in the flow drag/inertia ratio is accounted for by the first term, which is the only term present in the simple torsion pendulum model. Furthermore, the effects of the other Bessel functions are even more rapidly damped out than the major one. An additional important contribution to the damping term is the viscous drag of the cupula as it is displaced in the ampulla. As shown pictorially in Fig. 4 motion of the fluid in the canal is opposed by elastic restraining forces proportional to displacement of the cupula and a viscous force proportional to the rate of change of cupula angle. Steer demonstrates that the major portion of the system damping could be attributable to the drag of the cupula in the membranous ampulla, provided that the separation between the two be less than 10^{-4} cm. This assumes the following dimensions for canal and cupula, based on micrographs of Igarashi[7]

a = .15 mm (canal tube diameter)

B = 0.6 mm (radius of cupula)

ψ_1 = 0.6 rad (angular cross-section of cupula)

The wall separation is entirely consistent with injection micrographs of Groen et al.[8] Thus it would appear that the torsion pendulum model is sufficiently accurate to predict the mechanical dynamic response of the semicircular canals, but that the rationale behind it, i.e., attributing the drag solely to viscosity, is in error in neglecting the force necessary to slide the cupula in the ampulla.

A significant body of experimental evidence supporting the semicircular canal model was summarized by Groen in his comprehensive review in 1956.[9] These articles and the clear exposition by Cawthorne et al in the same year emphasized the system response to transient inputs. More recently Jones et al at McGill, Hixson, Niven, Guedry et al at Pensacola, Cappell at the Franklin Institute, Mayne, and our group at M.I.T. have emphasized the systems aspects of the semicircular canal response and pursued its analysis in the frequency domain.

The torsion pendulum equation written in Laplace transform notation, relating cupula deflection to head angular acceleration, is

$$\frac{\xi(s)}{\alpha(s)} = \frac{1}{s^2 + \frac{\pi}{\theta}s + \frac{\Delta}{\theta}}$$

If the roots of the denominator are real and widely separated (i.e., the system overdamped and $\Delta/\pi << \pi/\theta$), the equation may be approximated as

$$\frac{\xi(s)}{\alpha(s)} = \frac{1}{(s + a)(s + b)}$$

where

$a = \frac{\Delta}{\pi}$ (0.04 to 0.2 rad/sec)

[$a_{nominal}$ = 0.1 rad/sec for lateral canals, 0.14 rad/sec for posterior and superior canals]

corresponding to the long time constant of the cupula return phase

and

$$b = \frac{\pi}{\theta} \quad (4 \text{ to } 300 \text{ rad/sec})$$

$$[b_{nominal} = 10 \text{ rad/sec}]$$

corresponding to the short time constant of the system

Impulse Response

The torsion pendulum model predicts that the response to a sudden impulse of acceleration or step of velocity γ rad/sec (or sudden stopping of the skull after prolonged rotation at constant angular velocity) would be

$$\xi(t) = \gamma \frac{\theta}{\pi} (e^{-\frac{\Delta}{\pi}t} - e^{-\frac{\pi}{\theta}t})$$

The cupula response is a rapid deflection, with time constant θ/π, to a maximum of θ/π times the impulse, followed by an exponential decay back to zero with time constant π/Δ. The time required for the cupula deflection to return to any given constant level, such as a threshold angle ξ_{th} is given by

$$T = \frac{\pi}{\Delta} \ln \left(\frac{\theta\gamma}{\pi\xi_{th}}\right)$$

From the first exposition of the torsion pendulum model, reference was made to duration of subjective sensation of rotation following an impulsive stop. Notice that the logarithmic relationship between the duration of post-rotation nystagmus and the strength of the impulse or original angular velocity, γ, has a slope which depends only on π/Δ or the ratio of drag to elastic restraining force. However, the overall duration time depends upon the threshold for cupula deflection (which can be expressed in terms of minimum detectable angular velocity impulse). This assumption of sensation of rotation indicating cupula deflection is examined further in the adaptation model considered below. This relationship leads to the use of the cupulogram or impulsive stop experiments which are useful clinically, and which yield generally constant slope of time duration vs. log angular velocity, for angular velocity steps from threshold (approximately 2°/sec) up to 60°/sec. When subjective angular velocity is tracked during the experiment or indeed the angular velocity of slow-phase vestibular nystagmus (both of which were assumed proportional to cupula displacement), yet another check on the model is achieved for the same type of experiment. Additionally, Cawthorne et al tracked the oculogyral illusion psychophysically during post-rotation sensation.[10] Fig. 5 indicates typical experimental results of these three tests showing good agreement with the model prediction of straight lines on semi-log plots. Of considerable curiosity, however, is the consistent difference in the ratio π/Δ, or the slope of the cupulogram line, depending upon whether nystagmus (objective) or subjective angular velocity measurements are used. This will be discussed further below in treating adaptation.

(The difference in slope between the oculogyral illusion and sensation of rotation as seen in Fig. 5 is probably an artifact of the OGI tracking method and is not seen in Howard and Templeton.[11]

Step Response of Torsion Pendulum Model

The simple model can also be tested by using steps of constant acceleration and observing the latency of sensation. If the subject is started from rest and rotated at a constant angular acceleration α rad/sec^2, the model prediction of cupula deviation is

$$\xi(t) = \alpha \frac{\theta}{\Delta}(1 - e^{-\frac{\Delta}{\pi}t})$$

neglecting the influence of the short time constant. Solution of this equation for the time required for the cupula to exceed threshold yields testable predictions.

Meiry showed that the time to detect angular acceleration varied generally with the magnitude of the acceleration according to the torsion pendulum formula over the range 0.1°/sec^2 to 10°/sec^2.[1] Agreement is good over most of the range, with times slightly shorter than predicted near threshold accelerations. Meiry established vertical canal thresholds of 0.5°/sec^2 which are considerably higher than the horizontal thresholds of approximately 0.14°/sec^2. A comprehensive review of the data on response to angular acceleration was recently published by Clark.[12]

Sinusoidal Stimulation

A favorite test technique used in the field of feedback control systems is the utilization of a sinusoidal forcing function. Since the torsion pendulum model is linear except for the threshold phenomenon, it is amenable to analysis by such frequency response methods.

The torsion pendulum model predicts that ξ should be in phase with acceleration (leading velocity by 90°) at very low frequencies, in phase with velocity at the natural frequency ($\omega_0 = \sqrt{\Delta/\theta}$) and finally lagging velocity by nearly 90° at very high frequencies. The wide separation of the natural frequencies of the semicircular canal results in an extensive frequency range in which the cupula displacement is approximately in phase with the angular velocity of the head. Since this covers much of the frequency range encountered in normal daily activities (not including such artificial activities as prolonged spins), Jones and Milsum,[13] Mayne,[14] and others have stressed the behavior of the semicircular canals as velocity transducers. It must be remembered, however, that they are indeed velocity transducers only over the mid-frequency range. In attempting to determine the exact 90° phase lag point by the torsion swing experiment, Van Egmond et al have found an average value of 1 rad/sec, thus

$$\frac{\Delta}{\theta} \approx 1.0 \text{ sec}^{-2} \pm 20\%$$

Meiry explored the phase relationships in vestibular nystagmus to sinusoidal oscillations over the frequency range 0.2 to 10 rad/sec, using peak input amplitudes of 10° over most of this range. The phase relationships agree generally with the model based on the torsion pendulum approximation, assuming that instantaneous angular velocity of the slow phase nystagmus is proportional to cupula displacement.[15]

A typical vestibular nystagmus record is obtained by photoelectric measurement of horizontal eye position for rotation about the vertical axis (see Fig. 6). By eliminating the fast phase of nystagmus, the smooth portions can be fitted together to form the "cumulative eye position," whose phase with respect to the instantaneous simulator position is easily measured. The frequency response of vestibular slow phase nystagmus, in terms of eye velocity with respect to input velocity, is approximated by the relationship

$$\frac{\text{eye velocity}}{\text{input velocity}} = \frac{-3.2s}{(8s + 1)(0.04s + 1)}$$

Adaptation and Habituation

A persistent difficulty with the simple torsion pendulum model, which has concerned investigators for many years, is the lack of a suitable explanation of adaptation or habituation. (Adaptation is the decreased sensitivity to a continuing stimulus, whereas habituation refers to the decreased sensitivity to a repeated stimulus pattern.) A consistent difference appears in the torsion pendulum parameters depending upon whether they are estimated from eye movement recording or from subjective sensation of rotation. In particular, Groen[9] and others point out that the long period time constant (cupula return phase) is estimated at approximately 10 sec for the lateral canal in subjective cupulometry, but it appears closer to 16 sec based on the nystagmus cupulogram. Since both the subjective sensation of rotation and the angular velocity of slow phase nystagmus are theoretically proportional to cupula displacement, they should both follow the same time course of decay until passing through their respective threshold levels, and they should indicate the same cupula dynamics. Adaptation and habituation could occur centrally or peripherally.

The neuroanatomical pathways from the vestibular system to oculomotor control and to the cerebellum show branching of pathways at the vestibular and oculomotor nuclei. We assume that some of the adaptation and habituation apparent in the subjective response should be lacking in the more direct path of the vestibular-ocular loop. It is particularly instructive to examine the data of Hulk and Jongkees[16] and the experimental results obtained by Guedry and Lauver[17] measuring the sensation of angular velocity in response to steps of angular acceleration. Whereas the nystagmus response to a step in acceleration generally follows the torsion pendulum model, rising exponentially to a constant level, the subjective response begins to decrease after 20 to 30 sec of constant stimulation. These observations, combined with the

consistent differences between the frequency response phase lags of subjective and objective measurements led us to a first model for adaptation in the semicircular canal--subjective sensation of rotation--nystagmus pathways, shown in Fig. 7. This preliminary model recognizes that the cupula response signal undergoes more central processing in the subjective loop than in the nystagmus loop. In particular, Young and Oman include a pure delay time of 0.3 sec and linear adaptation dynamics of the form $s/(s + .033)$ as well as the threshold non-linearity. The adaptation dynamics represent a simple exponential decay with time constant of 30 sec in response to a steady stimulation or cupula deflection angle. Fig. 8 illustrates the model response of subjective velocity and nystagmus to a sudden increase in angular velocity such as used in the cupulogram impulse test. The nystagmus curve follows the cupula model, decaying with a long time constant of 16 sec. The subjective angular velocity, based on the same cupula deflection, exhibits a different transient behavior, returning to zero and overshooting slightly before finally decaying. When the nystagmus data taken for several different impulse heights is examined in terms of the duration of post-rotation nystagmus or time until the curve passes below threshold, it would of course indicate a long time constant of 16 sec. If the subjective angular velocity data is similarly treated, however, and the time duration estimated as though the entire system were second order, the apparent time constant is approximately 10 sec. These two numbers agree very closely with the observed objective and subjective time constants derived from cupulometry. The effect of the adaptation in the subjective loop is to shorten the apparent (second order) subjective time constant. Notice also that the linear subjective response overshoots, and if the magnitude of the overshoot is sufficient to exceed threshold, a "second effect" or subjective reversal would be predicted. This reversal has been noted many times, and it is possibly explained by the effect of the adaptation. The actual time constant of adaptation, incidentally, has relatively little effect on the apparent time constant of the subjective response. The frequency response of the linearized semicircular canal model including the adaptation and dead time is given in Fig. 9. This frequency response is very similar to the frequency response of the simple torsion pendulum model as used to match nystagmus data for frequencies in the range 0.1 to 2 rad/sec where nearly all of the test results lie. For very low frequencies, however, the model predicts even greater phase lead and lower amplitude ratio than the torsion pendulum model. Sinusoidal response data is not now available at these frequencies; however, these predictions are consistent with the observed transient responses for long durations. Although the differences between subjective and objective phase lag to sinusoidal stimulation in the region of 0.1 to 2 rad/sec is small, the presence of the pure delay in the subjective path does introduce more phase lag for subjective than for objective responses, in agreement with our experimental findings.

Having verified that the adaptation model produces generally correct responses to sinusoidal

and acceleration impulse stimuli, it remained to check it against higher order inputs. For consideration of long duration steps of angular acceleration, Guedry and Lauver's data were available to check the model. As seen in Fig. 10, the shape of the transient data generally agrees with the model for both nystagmus response and subjective sensation, although the magnitude of the experimental subjective velocity was higher than usually obtained by approximately 50%. Some long term adaptation effects may also be evident in the nystagmus data. The same type of input is used to determine the latency time to sensation of rotation for constant angular acceleration. The model match with experimental data of Meiry[1] and of Clark and Stewart[1H] is very good except at very low accelerations, as seen in Fig. 11.

One set of data which is not matched by the subjective response adaptation model is the duration of sensation following a step from very high angular velocities. Since the linear model response to a velocity step crosses zero, it predicts a maximum duration of post-rotation sensation of approximately 20 sec, whereas Van Egmond et al show data indicating durations of over 35 sec for 50-60°/sec velocity steps.

It is important to remember that this semi-circular canal adaptation model applies only to decreased subjective response to steady stimulation. It does not attempt to deal with the fascinating and practical problem of habituation to repeated stimulus patterns. "Vestibular training" of pilots, acrobats, ice skaters, and others undoubtedly involves such learning, in which familiar vestibular response patterns are recognized and suppressed. The difference in subjective sensation between jumping off a stair and descending suddenly in an elevator is an obvious example of CNS habituation, perhaps through the "efferent copy" mechanism.

OTOLITHS

Physical Characteristics

Each non-auditory labyrinth in man contains two otoliths of uncertain function, the utricle lying near the junction of the semicircular canals and the saccule slightly below. The utricular otolith is shown schematically in Fig. 12. The gelatinous mass labelled "otolith" contains many otoconia, or calcium carbonate crystals, giving it a density larger than the surrounding fluid. The otolith can slide over the macula, restrained by supporting hairs and sensory cells. The displacement is limited to approximately 0.1 mm, and the bending of the cells is transmitted as neural signals from the macula. Electrophysiological data on neural firing patterns by Adrian,[19] Lowenstein and Sand[20] and others reveals a partially adapting response to sustained tilt of the otolith with respect to the vertical.

Models of Otolith Function

There has been almost no intensive research into the precise physical-mechanism operation of the otoliths. Their structure does suggest an overdamped mass-spring-dashpot model linear accelerometer. The otoconia make the otolith denser than the surrounding fluid so that it is displaced by inertial reaction forces. The displacement is opposed by viscous forces associated with shear forces in the endolymph and with centering elastic restraint forces generated by the hair cells. Some measurements taken by de Vries[21] on fish otoliths support the model. Mayne[22] has postulated a third order term attributable to fluid pumping into a secondary chamber, but no physical evidence is available to support this notion. It is generally agreed that the sensing mechanism is bending of the hair cells, making the transducer responsive primarily to the shear components of acceleration defined with respect to the principal plane of the otolith, although compressive forces may also influence the otolith output. It is not clearly understood what the role of the saccule is in human orientation and postural control. Relatively large thresholds to sensation of tilt angle at orientations far from the upright indicate that the system is not symmetric along all three axes, but rather is optimized for the erect posture.

We have been working for several years on developing functional dynamic models of the non-visual gravireceptors and checking the models with behavioral experiments. Young proposed a single second order structure with acceleration and jerk terms in 1963.[3] Meiry performed a number of pioneering control experiments using pure linear acceleration stimuli, especially acceleration steps and sinusoids.[1]

At the suggestions of Dr. H. Von Gierke, a static component was included in the otolith model.* The revised linear model, which allows steady state response to acceleration, is shown in Fig. 13. This model represents only one axis of the three axis system, responding to the lateral component of specific force.

This revised linear model will act approximately as a velocity transducer over the mid-frequency range (0.19 < ω < 1.5 rad/sec). The transfer function from specific force to perceived tilt or lateral acceleration has a static sensitivity of 0.4.

The amplitude ratio and phase vs. frequency for the revised model is shown in Fig. 14, along with Meiry's experimental phase data on the relation between perceived linear velocity and actual horizontal sinusoidal velocity. The fit to the experimental data is excellent, although it clearly indicates the need for additional experiments at

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*   The remainder of this section is based on the paper, "A Revised Dynamic Otolith Model," by L. R. Young and J. L. Meiry, presented at the Third Symposium on the Role of the Vestibular Organs in Space Exploration, Pensacola, Florida, January 1967.

frequencies below 0.2 rad/sec to verify the pre-dicted drop in phase lead.

Recent supporting evidence for this model was provided by Kellogg[23] based on dynamic counterrol-ling experiments. The magnitude and phase lag of the torsional rotation of the eye was measured versus lateral head tilt for constant velocity rotation about a horizontal axis at various rates. The counterrolling points shown in Fig. 14 were taken from Kellogg's curve fit data for two sub-jects, each rotated clockwise and counterclockwise at rates from 5 to 30 rpm. Notice the overall agreement of the counterrolling phase lag data with the otolith model over the region tested. The amplitude ratio of the counterrolling data, related to the otolith model by an arbitrary counterrolling index, shows a decrease in the vicinity of the model break frequency at 1.5 rad/sec. Extension of the dynamic counterrolling data to the region 0.1 to 2.0 rpm would be exceedingly useful. The known zero phase lag for static counterrolling was one reason for model revision.

The acceleration threshold in the revised model raised the problem of its physiological interpretation. On the one hand, the lead term in the transfer function could be attributed to a more complex mechanical model of the otolith, perhaps including the effect of a second mass-spring-dashpot combination representing movement of the macula with respect to the bony structure. Mayne has independently explored this avenue and sug-gested a possible mechanical otolith model which combines aspects of a conventional accelerometer and an integrating accelerometer. On the other hand, the lead term could be attributed to the neurological end, either in central processing of otolith displacement signals or through the pres-ence of two types of hair cells in each macula; one responding to otolith displacement or hair bending, the other responding to rate of change of otolith displacement or rate of change of hair bending. Similarly, the hair cells could produce the lead term if they were of the slowly adapting type postulated by several researchers.

Because of its compatability with the time-to-threshold data, we favor the explanation of the lead term on the basis of neurological adaptation or processing of otolith displacement, rather than attributing it to the mechanical structure. The nonlinear otolith model is shown in Fig. 15. The threshold is here shown as based on a minimum deviation of the otolith with respect to the macula rather than a minimum output of the total model. The threshold level may be related to specific force, but not to otolith displacement at this time.

The ability of the nonlinear model to match data on latency time for perception of constant horizontal linear acceleration is shown in Fig. 16. The model assumed an absolute threshold of approxi-mately 0.005 g, which placed the 0.01 g latency time at 5 seconds as per the data point. The remainder of the model prediciton fits the data exceedingly well.

CROSS-COUPLING EFFECTS BETWEEN LINEAR AND ANGULAR SENSORS*

The notion that human vestibular perception of rotation is uniquely attributable to the semi-circular canal models, and perception of linear acceleration attributable only to the otoliths, is clearly an oversimplification. A tentative model used to tie together some of the data on vestibular cross-coupling between angular and linear accelera-tions is shown in Fig. 17. It was based on the following assumptions:

1. Lateral displacement of the otolith, corres-ponding to a shear component of specific force, produces an additive component of nystagmus with the slow phase in the direction of the otolith displacement (compensatory) and with sensitivity of the order of 10°/sec/g. We will call this linear acceleration sinsitive component "L-nystagmus."

2. The resulting eye movement nystagmus is deter-mined by the vector addition of the semi-circular canal and otolith contributions.

3. The semicircular canal contribution may be influenced by linear forces either through distension of the canal or by utricular inhibition.

The information upon which this model was developed came from a variety of sources and rep-resented a number of different types of investiga-tion. Since the data were primarily of the input-output variety (acceleration in, nystagmus out), the basis for assigning functions to the otoliths is relatively weak.

Vestibular nystagmus has characteristically been attributed to the stimulation of the semi-circular canals and explained teleologically in terms of the requirement for maintaining a "stable platform" of the eyes in space despite motion of the head. Most attempts to elicit vestibular nystagmus by stimulation of only the linear accel-eration sensors have met with equivocal results in the past.

In a set of controlled experiments using periodic linear acceleration stimuli in the hori-zontal plane, Niven et al[24] found consistent hori-zontal nystagmus corresponding to L-nystagmus of sensitivity 16 deg/sec/g.

Two separable effects can be observed when the vestibular system is subjected to prolonged stimu-lus by a rotating specific force. First of all one sees a cyclic modulation of nystagmus, more or less in phase with the component of specific force. This AC component can lead to reversal of nystagmus direction during part of the cycle, as noted by Benson and Bodin.[25] We attribute this portion to L-nystagmus and consider it a likely representation

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of the contribution of the otoliths to total eye
movement stabilization. In addition one notes
that the average nystagmus does not die out during
prolonged stimulation but rather remains at some
finite level consistent with the direction of
apparent rotation. This work was stimulated by
recent human experiments by Benson and Bodin and
by Correia and Guedry[26] followed by electrophysio-
logical measurements by Benson, Guedry, and Jones[27].

These "barbecue spit" experiments involved a
sinusoidal linear acceleration stimulus and a con-
stant angular velocity stimulus which would
normally give no prolonged vestibular nystagmus.
Steer induced this type of response by counterrota-
ting his subjects in a chair at the end of a 32 ft.
arm on the M.I.T. Instrumentation Laboratory
Precision Centrifuge. Using a rotating 0.3 g
acceleration vector, he produced the sinusoidal and
bias components of slow phase nystagmus. His
summary curve, including the "roller pump model"
prediction for bias, is given in Fig. 18.

Steer calculated the magnitude of a "roller
pump" action which would account for the steady
bias in nystagmus during a rotating linear accel-
eration stimulus and found it a feasible explana-
tion. This solution rests on three observations.
First, the membranous labyrinth is firmly attached
to the bony canals at the outer circumference but
is unsupported at the inner circumference. Second,
the density of the membranous labyrinth is greater
than that of the perilymph. Third, the membranous
labyrinth is relatively flexible. Thus, as shown
schematically in Fig. 19, the canal will be con-
stricted at the point that is instantaneously
"down," and this constriction will rotate around
the canal with a rotating linear acceleration stim-
ulus, pushing fluid ahead and deflecting the cupula.
The quantitative results of experiments carried out
thus far support such a theory, but far more
research on the subject remains to be done.

CONCLUSIONS

A summary of our current theories on bio-
cybernetic models of the human vestibular system is
given in Fig. 20. Even on the "black box"
modelling level, there are still many areas to be
filled in at this point. For semicircular canal
dynamics, the fluid dynamics analysis has shown the
simple torsion pendulum approach to account for
over 95% of the cupula response, and consequently
it is used as the model. However, the detailed
canal dynamics, inferred from nystagmus recordings,
are only known with confidence for the horizontal
canals. Careful electrophysiological recordings of
neural signals from each of the canals in a primate
would give more direct evidence as to the exact
break frequencies at the mechanical end organ, al-
though the precise numbers are probably of limited
interest. For the posterior and superior canals,
we assume that the actual mechanical break fre-
quency is somewhat less than the value of 0.14, de-
duced on the basis of a 7 sec time constant
observed in subjective responses. Although a
specific model is proposed for subjective angular
velocity adaptation in the case of lateral canal
stimulation, it must also be assumed that some

adaptation occurs for the other canals. In addi-
tion, slow adaptation undoubtedly also applies to
the nystagmus response in man, although this is
somewhat difficult to demonstrate consistently.
The models for the otolith system are based
primarily on perception of direction of motion and
measurement of counterrolling angle. It is assumed
that similar dynamics apply to the saggital axis,
or at least to the axis in the saggital plane
intersecting the plane of the flat part of the
utricular otolith. Models for dynamics along the
third orthogonal axis of the linear acceleration
system normal to the plane of the utricle (and
perhaps involving the saccules) remain nearly com-
pletely without supporting data in man at this
time. It is clear that in addition to the large
number of challenging neurophysiological problems
brought forth by this biocybernetic approach, there
remains a significant amount of work to be done by
the application of conventional control theory to
this multi-input, multi-output biological system.

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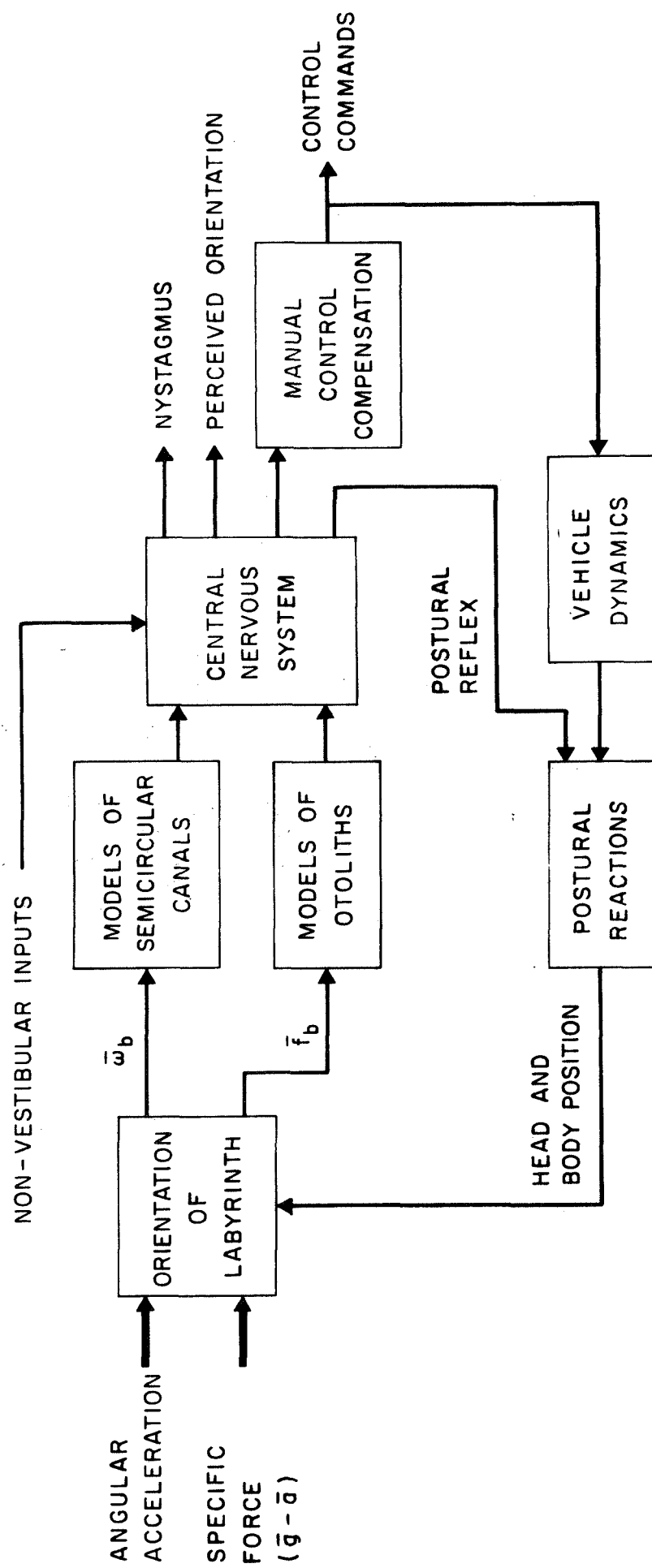
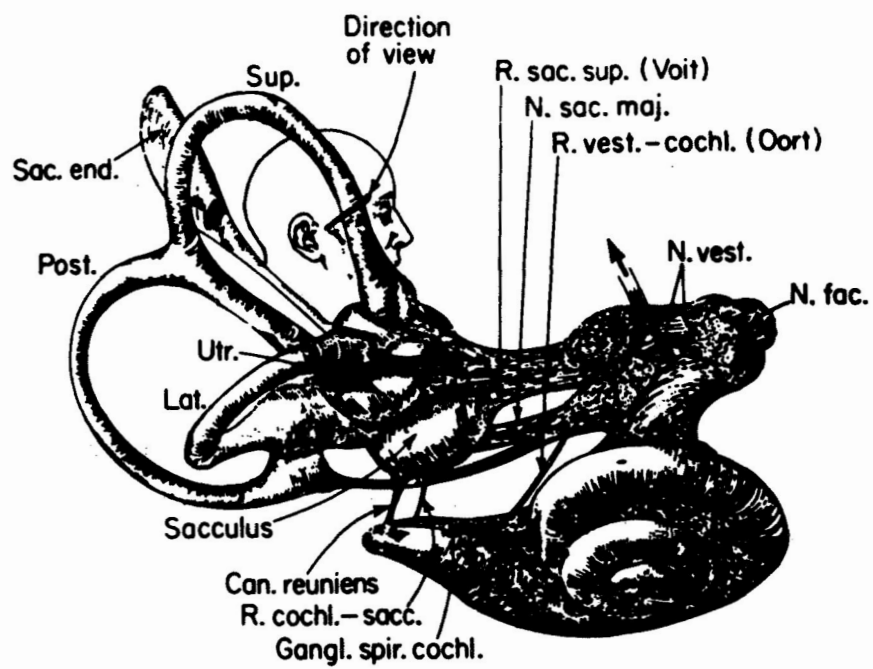Fig. 1 . Framework for Systems Analysis of Vestibular Function

Fig. 2.   The vestibular apparatus
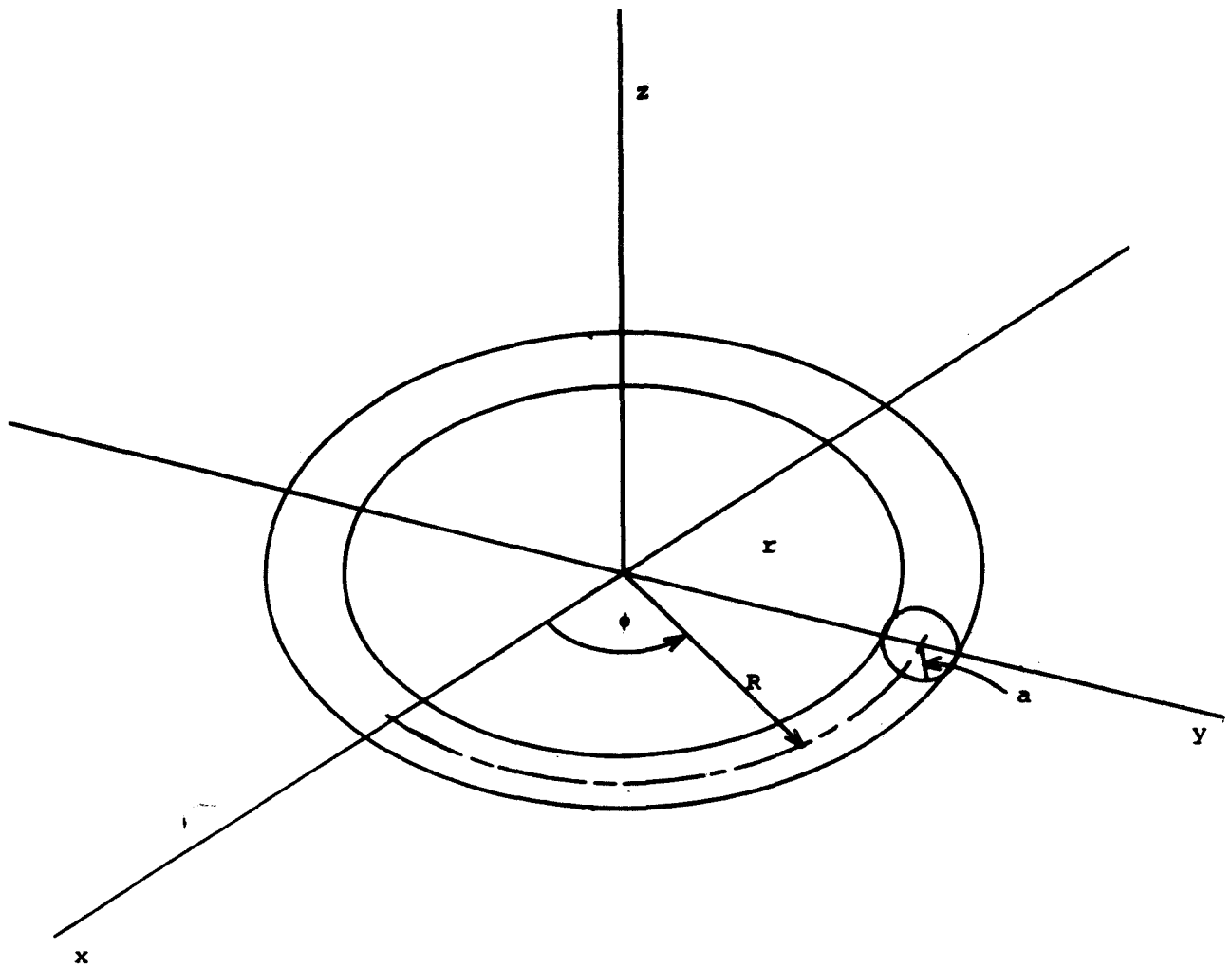
(from Fogel)

Fig. 3. Torus placement relative to a cylindrical
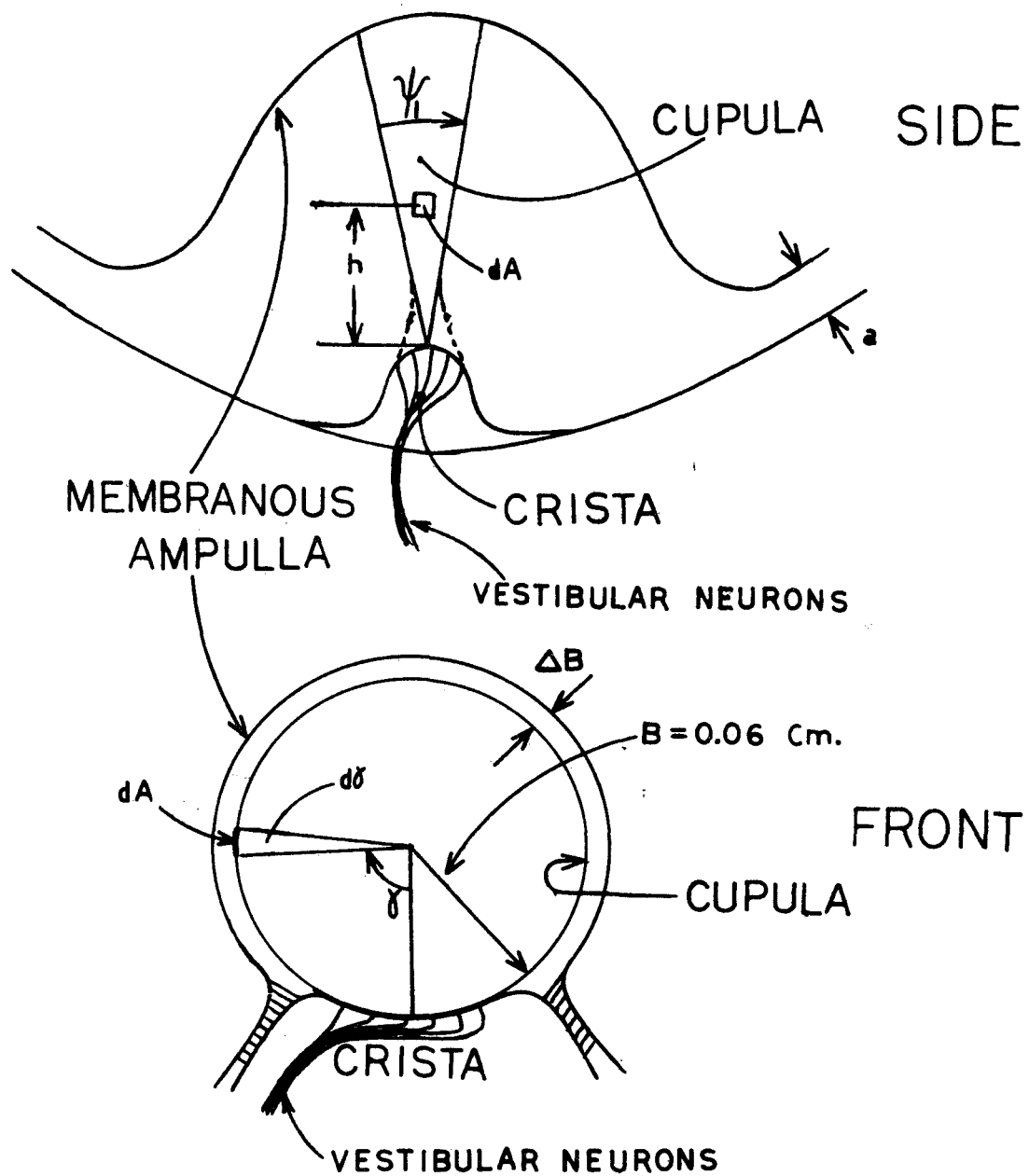coordinate system for calculation of its dynamics

(from Steer)

Figure 4
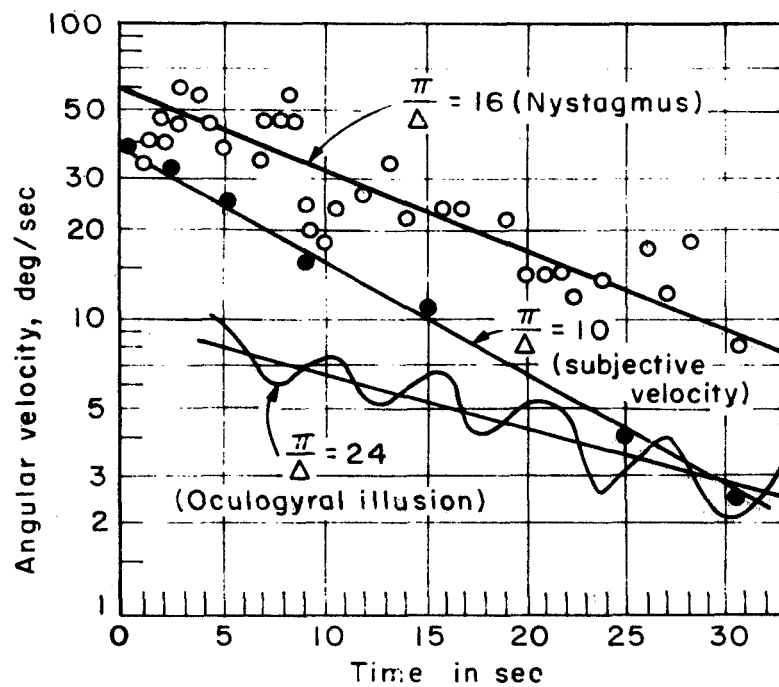
A physical model for the cupula

(from Steer)

Fig. 5   Time course following a sudden cessation
         of rotation

   a. Nystagmus - Groen, Lowenstein, Vendrick
   b. Subjective velocity - Van Egmond,
                            Groen, Jongkees
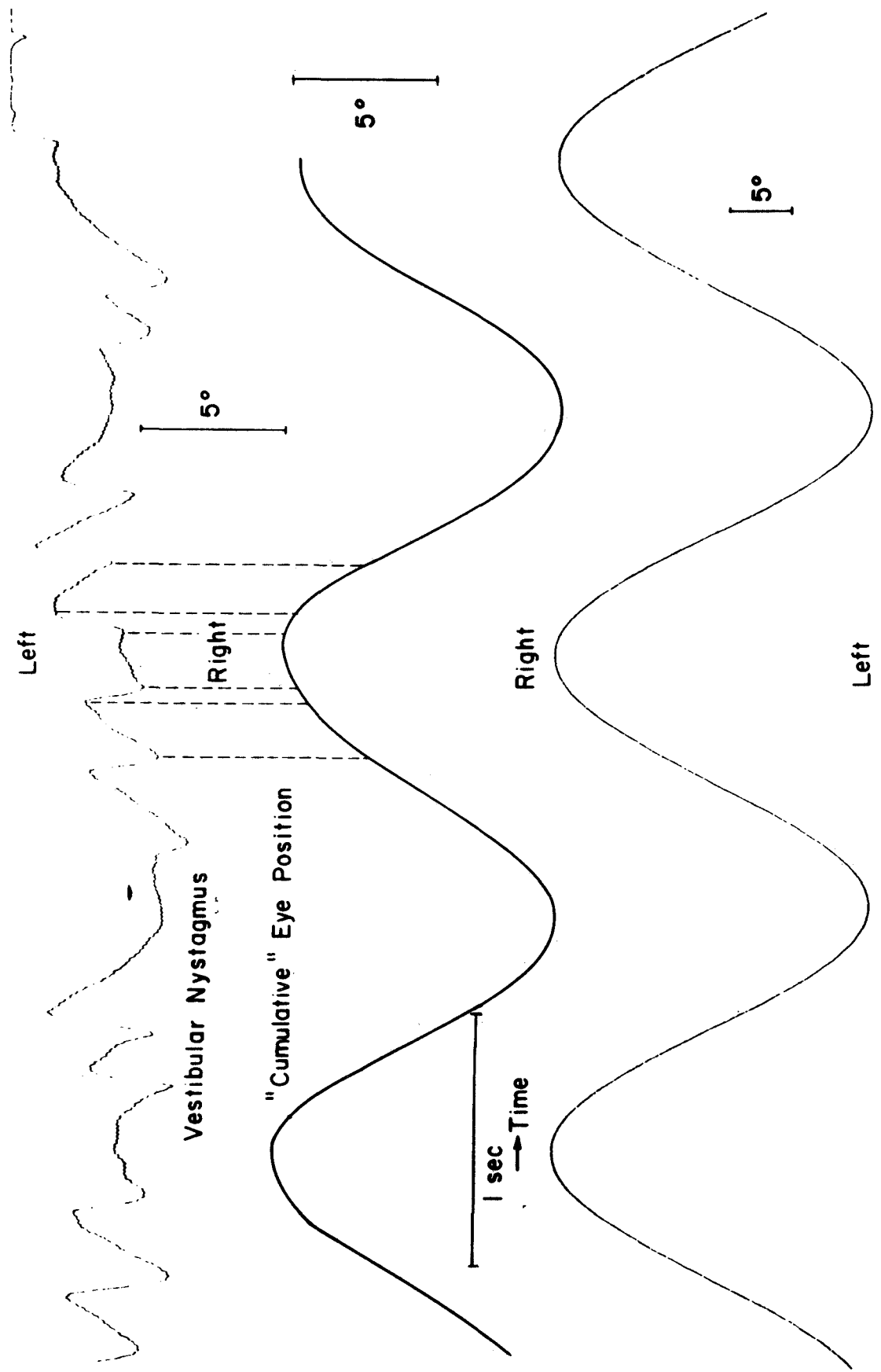   c. Oculogyral illusion - Cawthorne,
                            Hallpike, Hood, Dix

Fig 6 Vestibular Nystagmus And "Cumulative" Eye Position, f = 0.5 cps
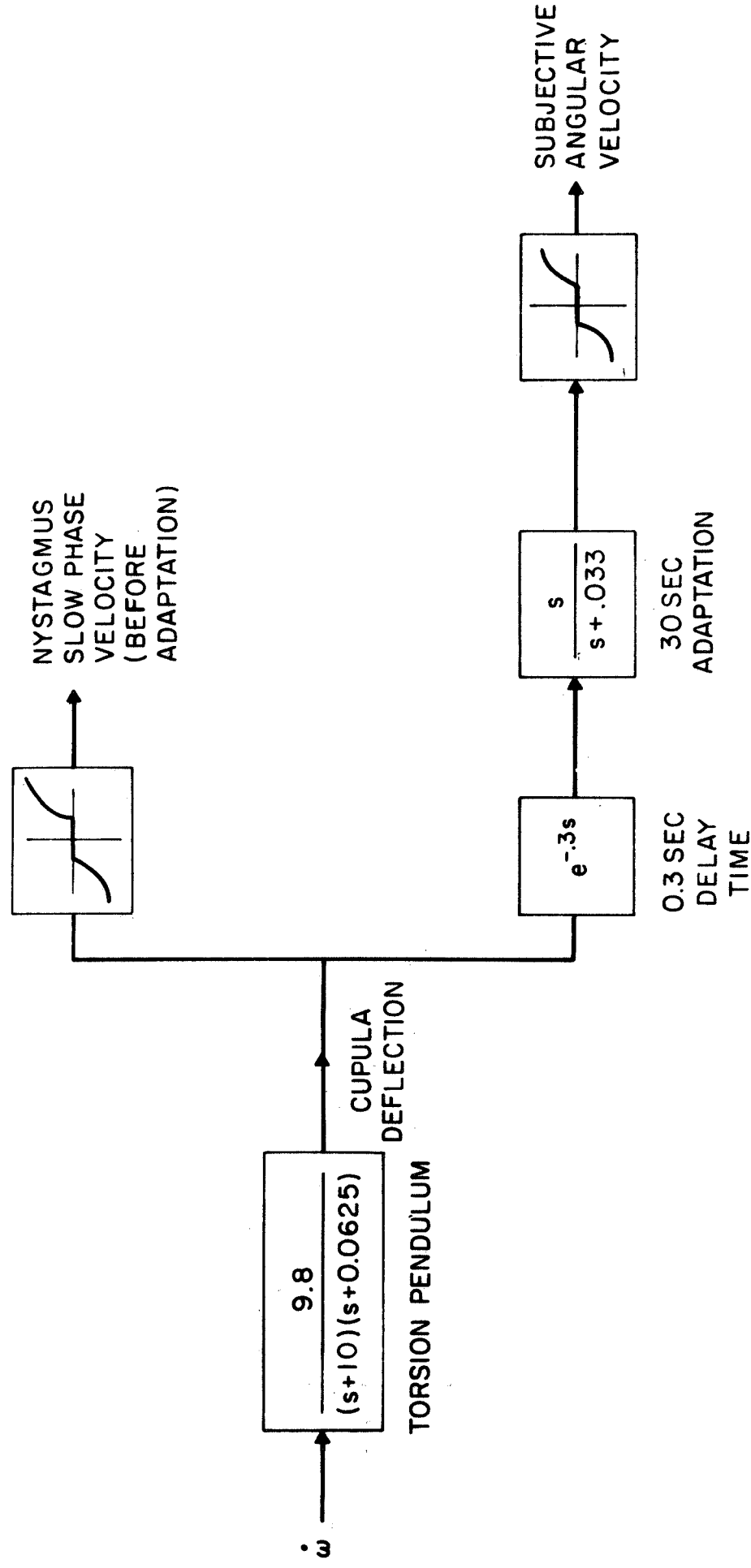Note the Correspondence of Slow Phase Vestibular Nystagmus and "Cumulative" Eye Position. (from Meiry)

Fig. 7   Model for Subjective and Nystagmus Response for Rotation About a Vertical Axis
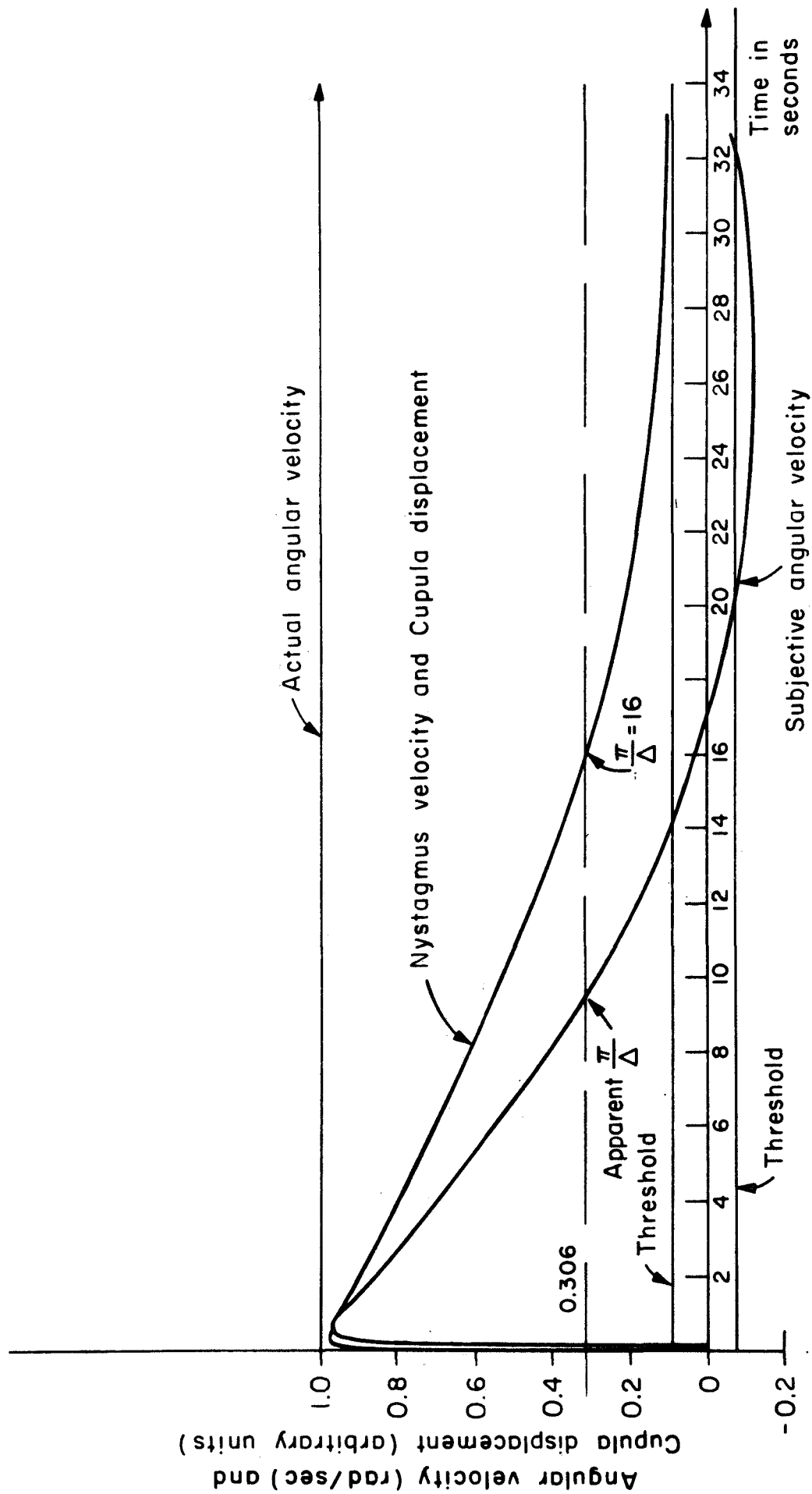
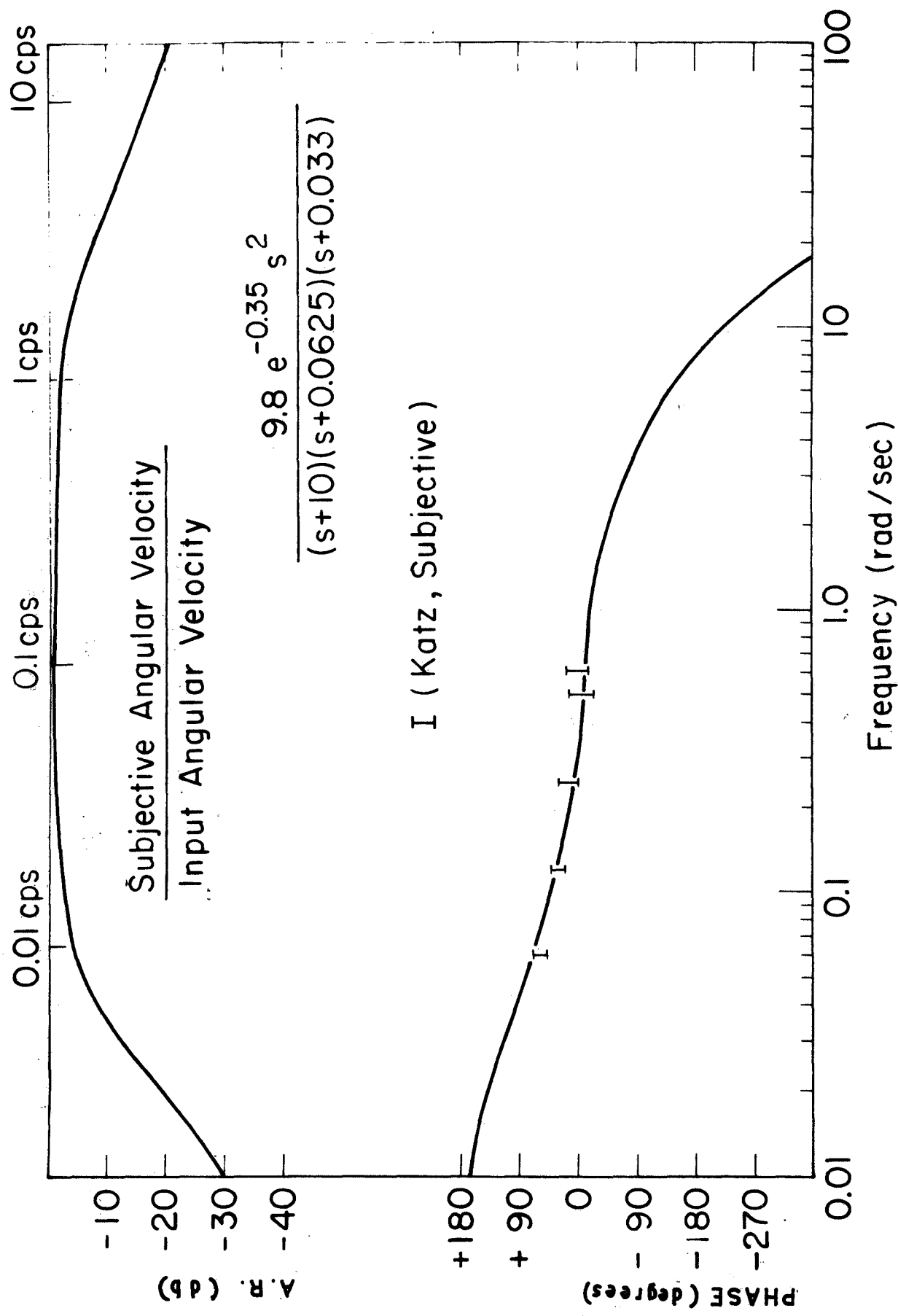Fig. 8   Velocity step response of extended semicircular canal model

$$\frac{\text{Subjective Angular Velocity}}{\text{Input Angular Velocity}}$$

$$\frac{9.8\ e^{-0.35}\ s^2}{(s+10)(s+0.0625)(s+0.033)}$$

I (Katz , Subjective)

Fig. 9   Frequency Response of Adaptation Model for Subjective Response
to Angular Acceleration
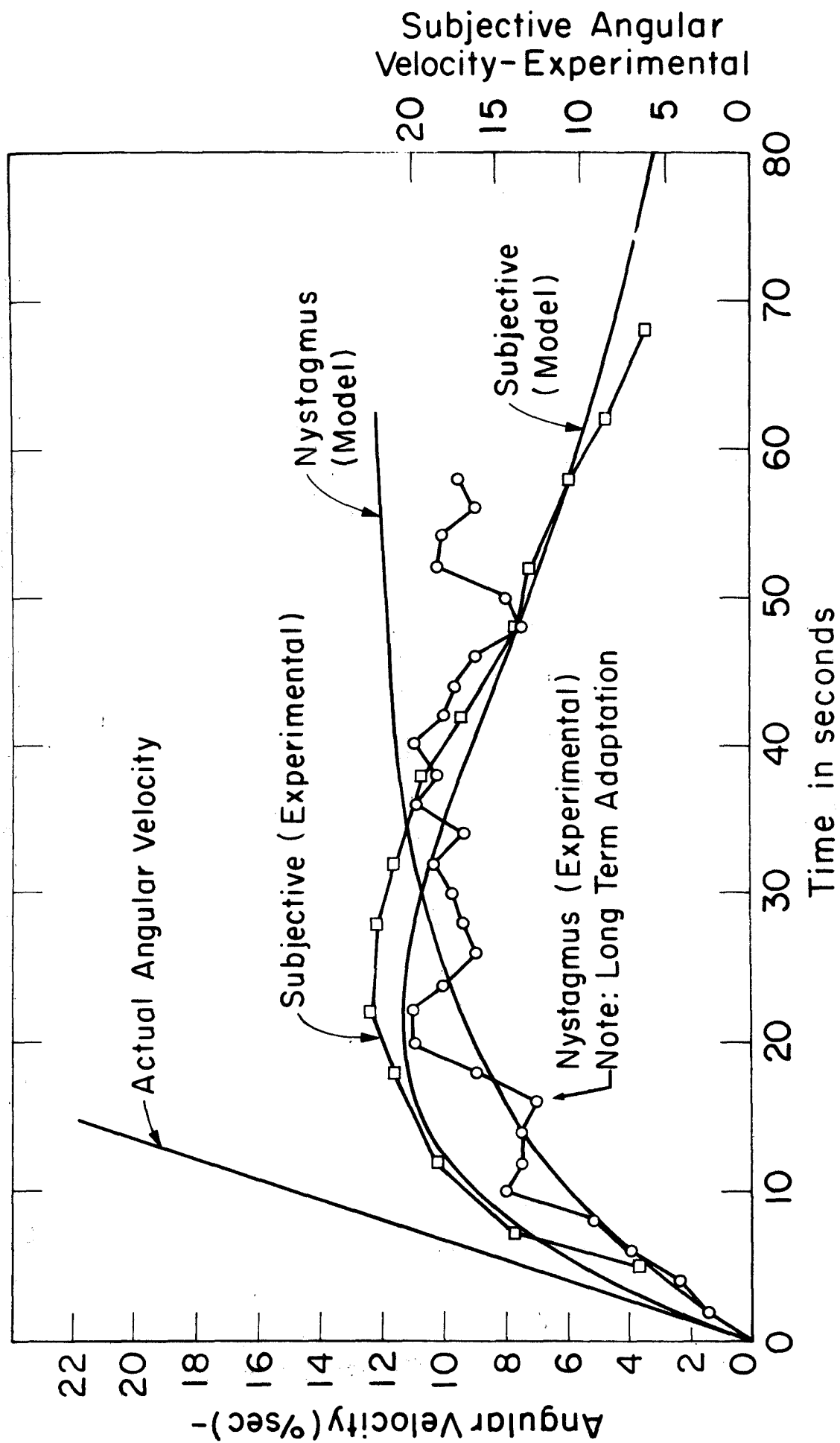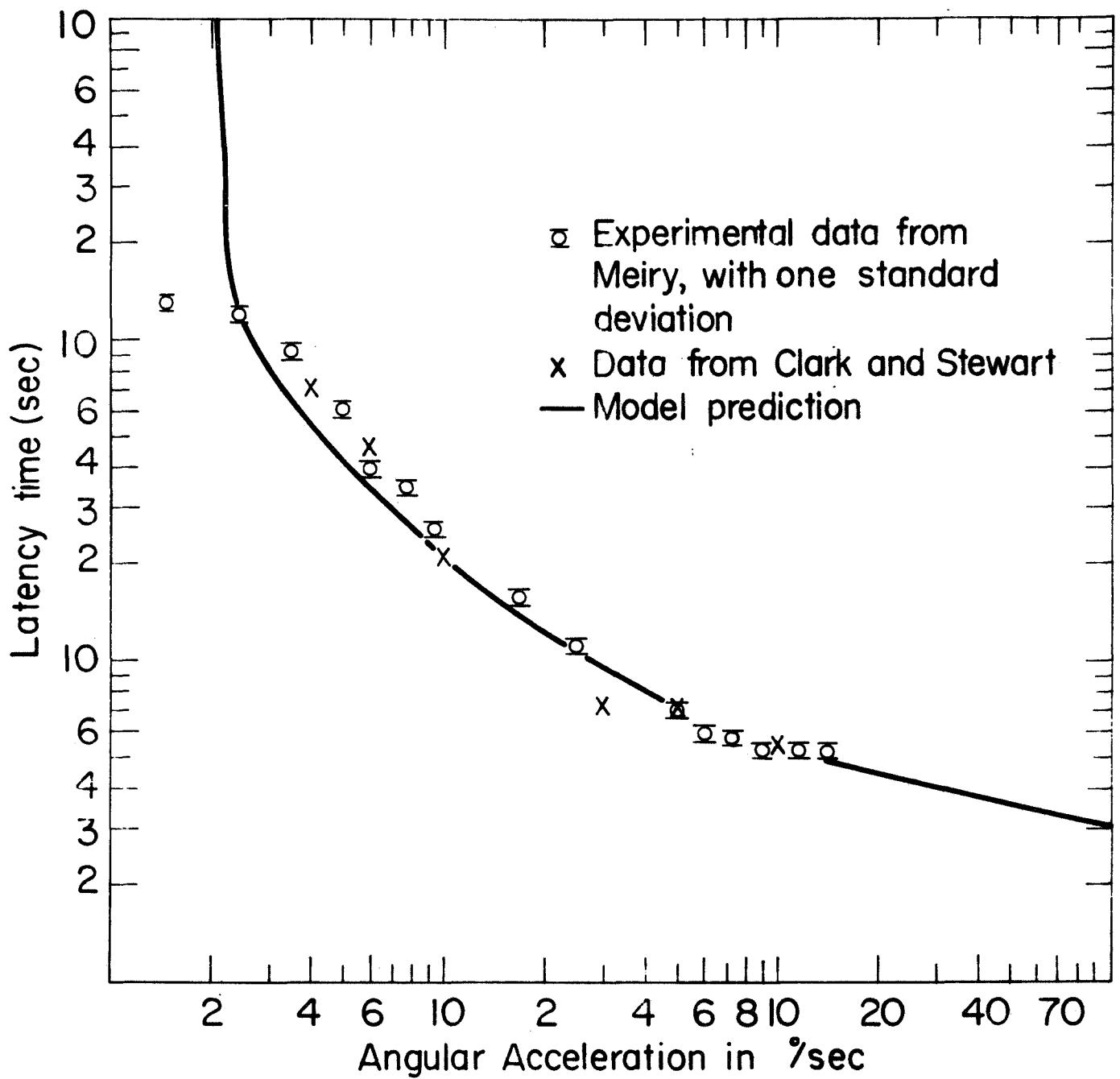
Fig. 10 Comparison of Adaptation Model of Vestibular Response with Guedry and Lauver Experiments for an Angular Acceleration Step

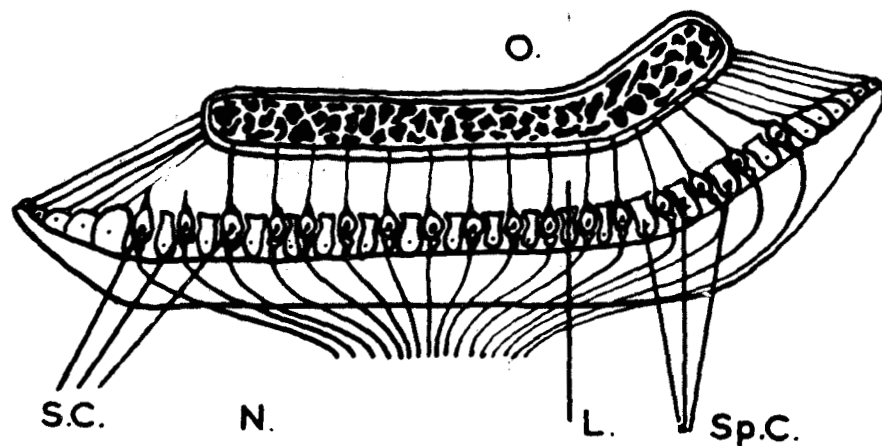Fig. II Adaptation model of semicircular canals

Fig. 12 . Schematic drawing of a cross section
of an otolith and its macula. O. is the otolith,
suspended by strands which run from the margins to
the macula, consisting of supporting cells (Sp.c)
and sensory cells (S.C.). Between the otolith
and the macula there is a thin layer (L.) to allow
the otolith to slide over the macula. N. is the
nerve. (from Groen et al)

SPECIFIC FORCE

MECHANICAL MODEL
OF OTOLITH
ACCELEROMETER

$$\frac{1.5}{(S+0.19)(S+1.5)}$$

OTOLITH
DISPLACEMENT
W.R.T. MACULA

d

MECHANICAL
THRESHOLD

NEURAL
PROCESSING
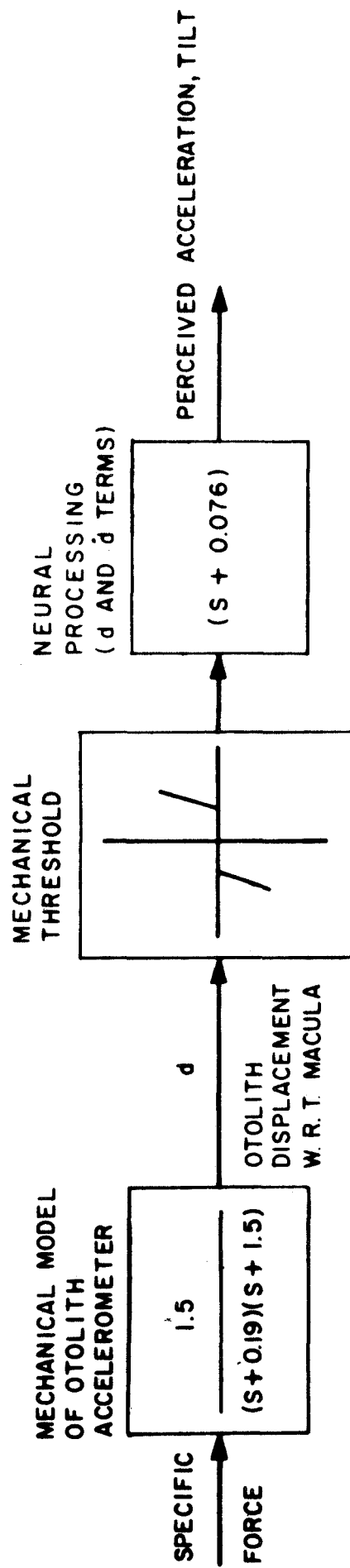(d AND d̊ TERMS)

$(S + 0.076)$

PERCEIVED ACCELERATION, TILT

Fig. 13.   REVISED NONLINEAR OTOLITH MODEL
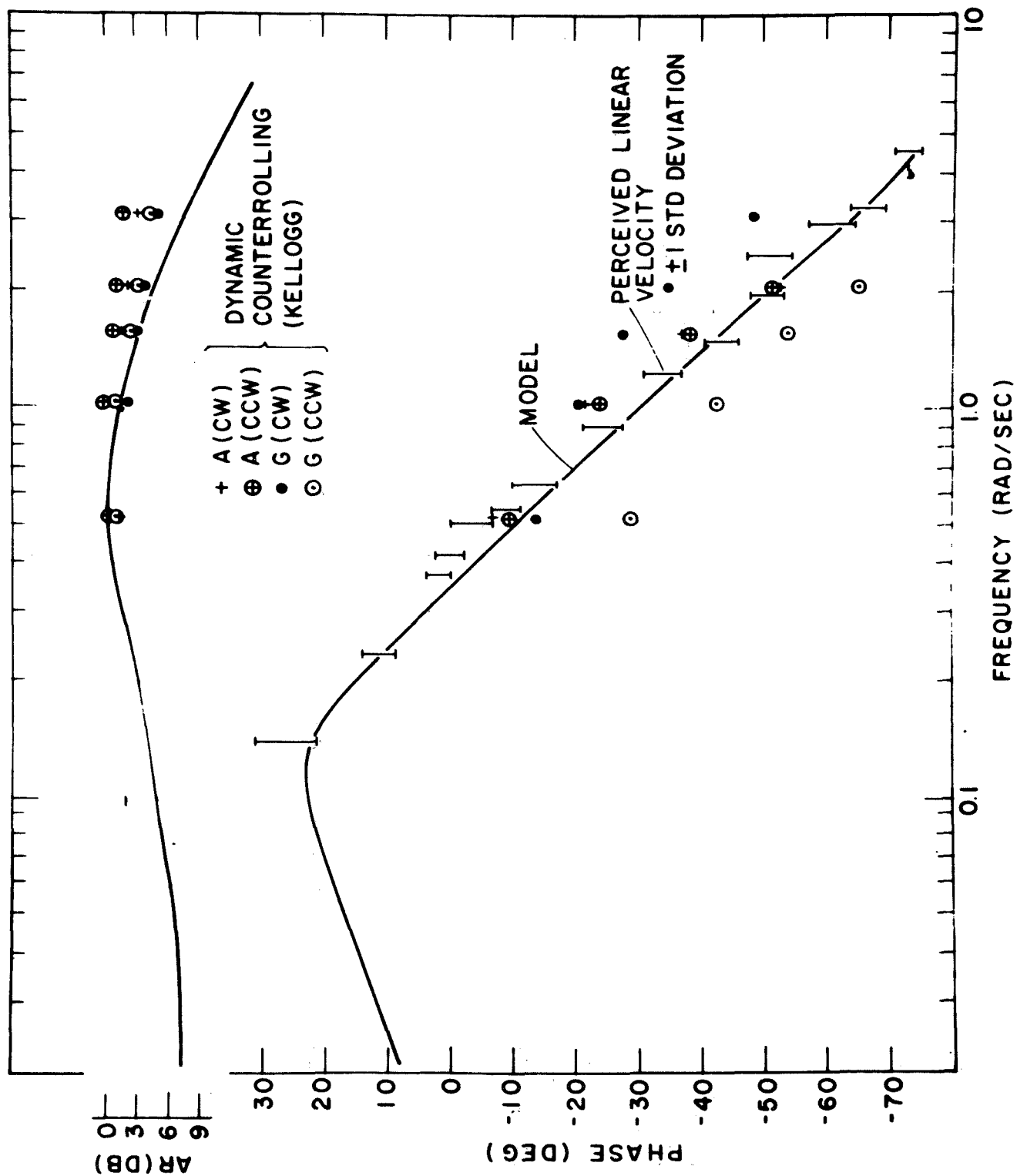
Fig. 14 PERCEIVED VELOCITY FREQUENCY RESPONSE

Fig. 15. REVISED NONLINEAR OTOLITH MODEL

$$\frac{1.5}{(S+0.19)(S+1.5)}$$

⊥ EXPT. DATA (±1 STD. DEVIATION)

— OTOLITH MODEL (MECH. ONLY)
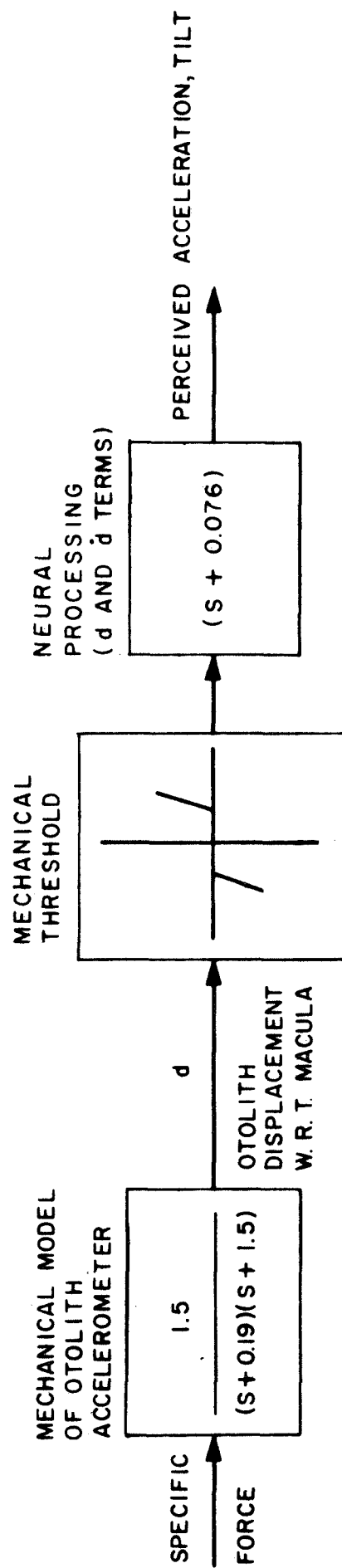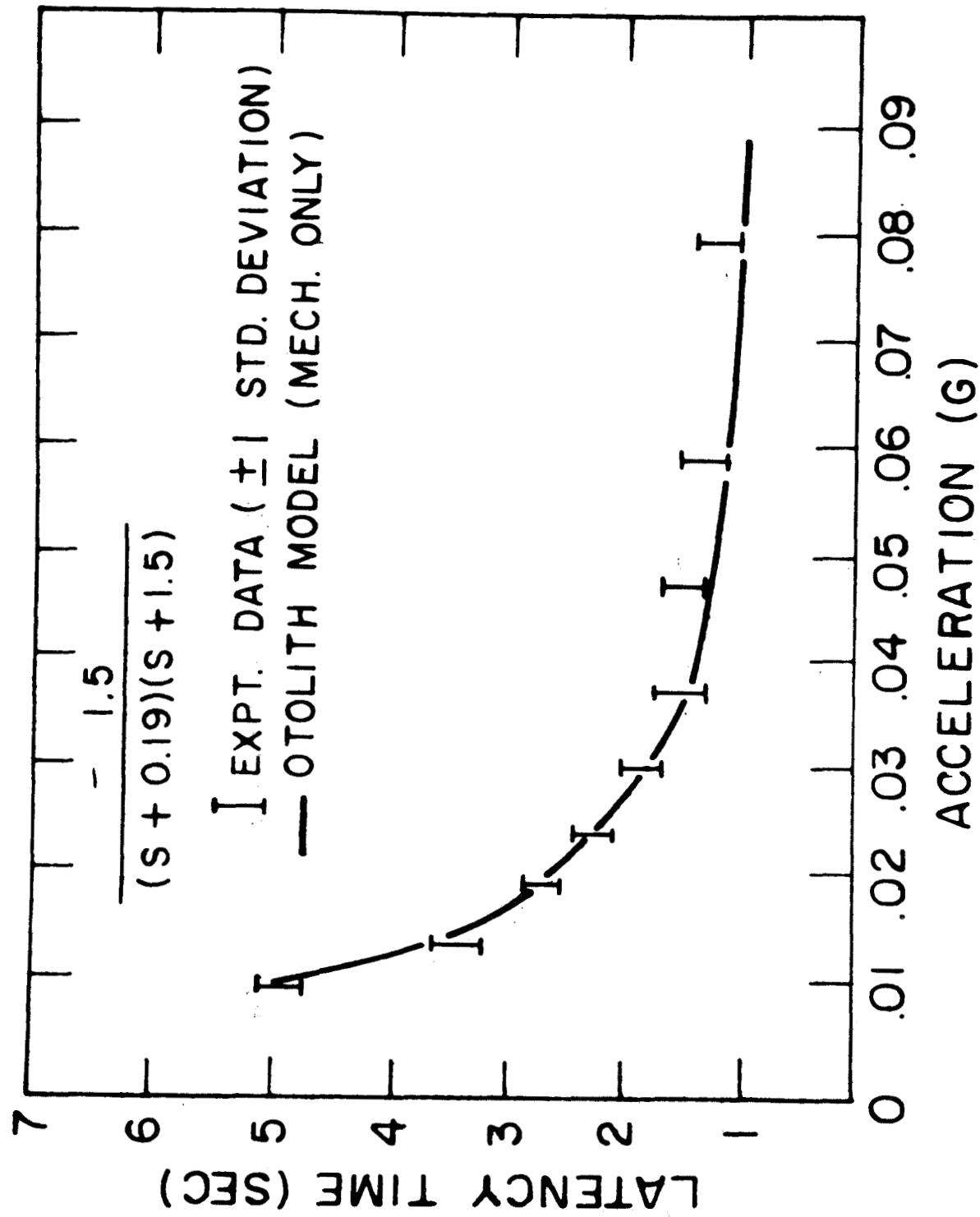
Fig. 16. TIME FOR PERCEPTION OF CONSTANT LINEAR ACCELERATION – MODEL AND EXPERIMENT
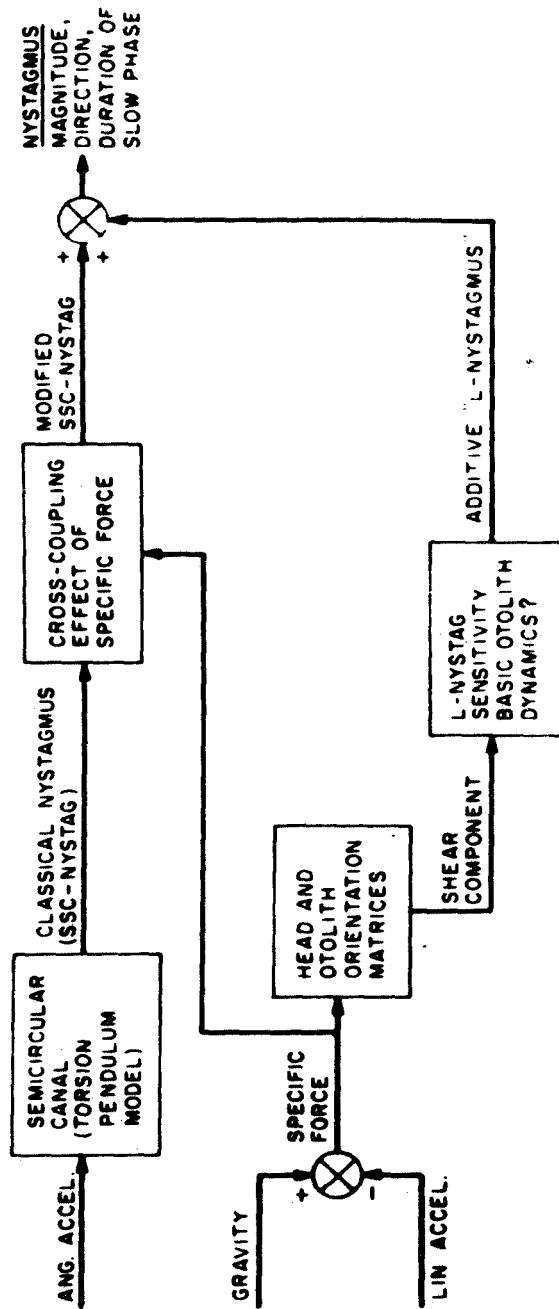
Fig. 17. PRELIMINARY STRUCTURE - MODEL OF INFLUENCE OF LINEAR ACCELERATION ON NYSTAGMUS
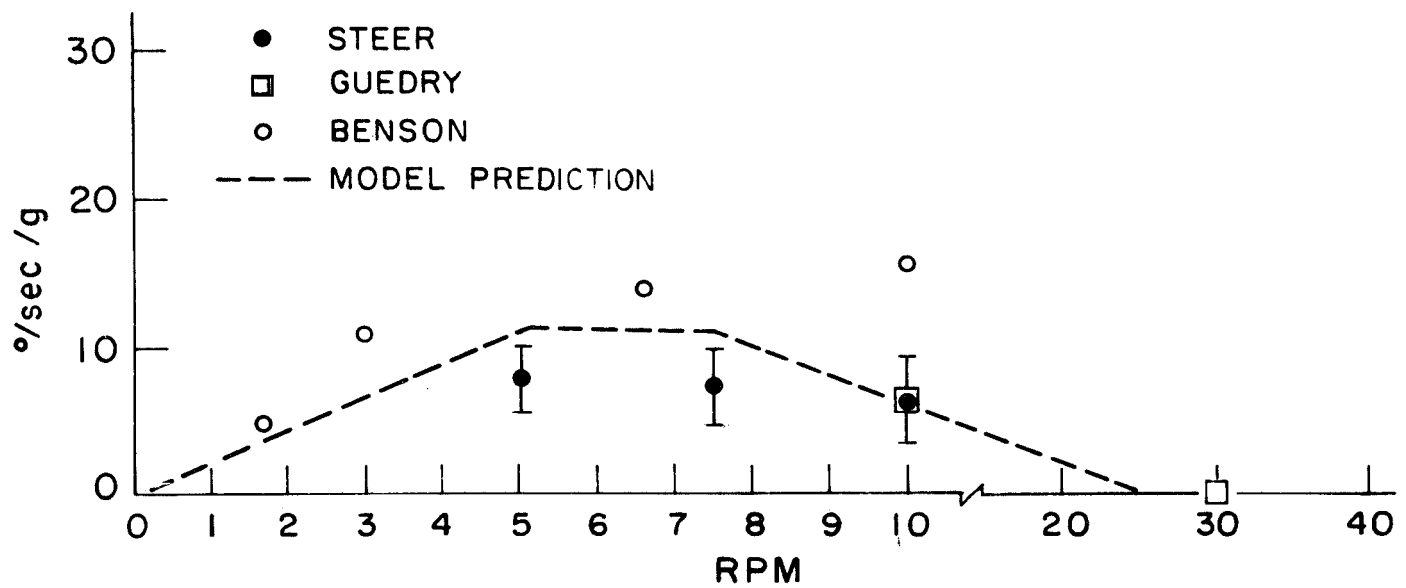
(a) Magnitude of Bias
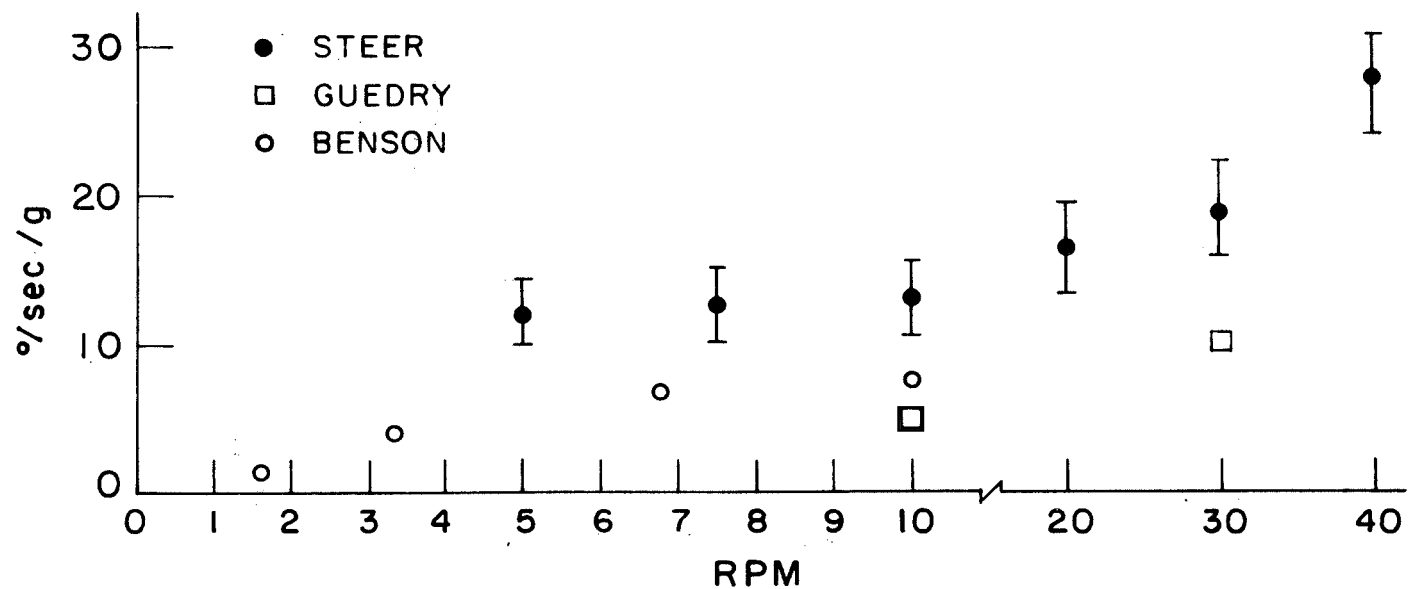
(b) Magnitude of Sinusoidal Component

(L-nystagmus)

Fig. 18 Summary of Available Data of Normalized Bias and Sinusoidal Amplitude of Vestibular Nystagmus from Rotation in a 1g Field
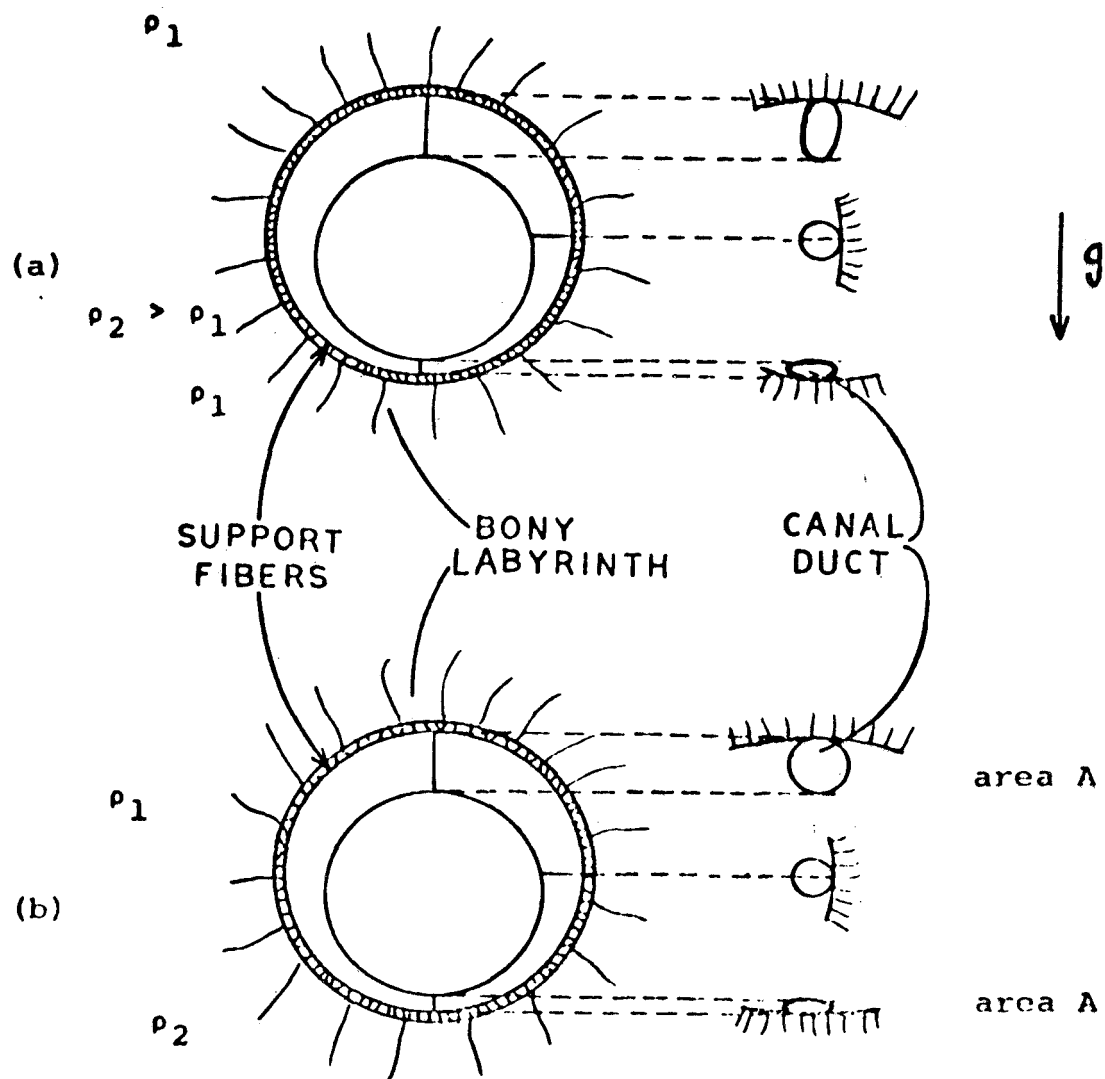
Figure 19

Distension of a flexible toroidal duct due to
the influence of gravity on the density of
the duct (a) or the density difference
between the fluids

(from Steer)

CANAL DYNAMICS†

$\bar{\omega}_{H-I}$ ANGULAR VELOCITY OF HEAD WITH RESPECT TO INERTIAL SPACE

ORIENTATION OF CANALS WITH RESPECT TO THE SKULL

$\omega_{L\,HOR}$ $\dfrac{9.8s}{(s+10)(s+0.062)}$

$\omega_{R\,HOR}$ "

$\omega_{L\,POST}$ $\dfrac{as}{(s+10)(s+0.14-x)}$ *

$\omega_{R\,SUP}$ "

$\omega_{L\,SUP}$ "

$\omega_{R\,POST}$ "

SYNERGISTIC SUM

~ 5 DEG/SEC THRESHOLD

$e^{-.3s}$ $\dfrac{s}{s+30}$

CNS DELAY   30 SEC HABITUATION THRESHOLD   ~2 DEG/SEC THRESHOLD

→ NYSTAGMUS SLOW PHASE VELOCITY (LATERAL)††

→ SUBJECTIVE ANGULAR VELOCITY (LATERAL)

? → NYSTAGMUS / SUBJECTIVE

? → NYSTAGMUS / SUBJECTIVE

OTOLITH DYNAMICS

$\bar{f}=(\bar{g}-\bar{a})$ SPECIFIC FORCE ON HEAD

ORIENTATION OF UTRICLE "PLANE" WITH RESPECT TO THE SKULL

$f_{L\,LAT}$ $\dfrac{1.5}{(s+0.19)(s+1.5)}$

$f_{R\,LAT}$ "

$f_{L\,SAG}$ "?"

$f_{R\,SAG}$ "?"

$f_{L\,COMP}$?

$f_{R\,COMP}$?

THRESHOLD EQUIVALENT TO 0.005 g's

NEURAL LEAD $\dfrac{s+0.076}{2}$ → PERCEIVED LATERAL ACCELERATION OR TILT (SMALL ANGLES)

~.03 → COUNTERROLLING ANGLE

† Neglecting higher order terms from fluid dynamics analysis.

†† Neglecting effect of linear acceleration on nystagmus.

* Habituation in vertical canal not yet quantified. Break frequency of 0.14 r/s based on long time constant (subjective) of 7 sec.
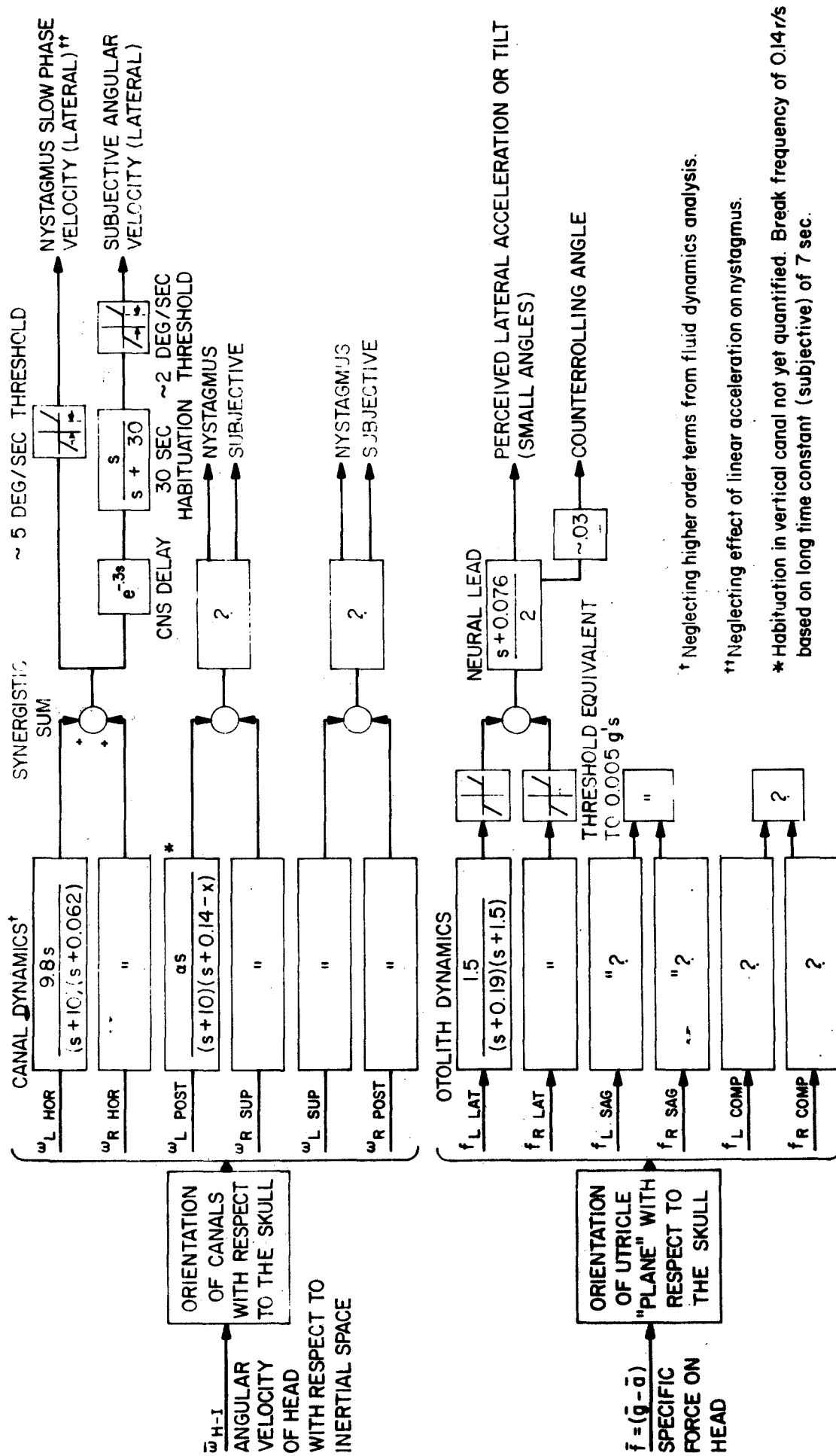
Fig. 20 Summary Diagram. Biocybernetic model of the vestibular system, 1968